CARCASS ANALYSIS OF WILD AND THERMAL-STRESSED DICKCISSELS¹

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Studies of weight fluctuations in birds have indicated that seasonally related changes in mass occur regularly in the adults (Baldwin and Kendeigh, 1938; Nice, 1938). The abrupt vernal and autumnal accumulation of fat in migrants has been well documented (Helms and Drury, 1960; King and Farner, 1959; Norris et al., 1957; Odum and Connell, 1956; Odum and Perkinson, 1951; Ward, 1963), and the causative factors involved have been experimentally investigated (Kendeigh, West, and Cox, 1960; King, 1961; Koch and De Bont, 1951; Lofts and Marshall, 1960; Odum and Major, 1956; Schildmacher and Steubing, 1952). Few data, however, are available on lipid levels at other times of the year or on the amounts of water and protein at any season.

The Dickeissel (*Spiza americana*) nests in North America during the summer months, arriving in the southern part of its breeding range along the coast of Texas in April and reaching its northern nesting limit on the Great Plains in June. From late August to October the Dickeissel migrates to its tropical wintering area, which extends from 19° N in Mexico to 5° N in northern South America.

This paper is a report of the amounts of the major body constituents of wild Dickeissels throughout most of the year, and the effect of thermal stress at both extremes of its tolerable temperature range on these levels.

METHODS

Most birds were captured with Japanese mist nets, but some additional individuals were shot. Summer birds were obtained during 1961 and 1962 in Piatt and Champaign Counties, Illinois, and winter birds were collected from flocks near Tocumen and Pacora, Republic of Panama, in January and February 1961. Spring migrants were secured from flocks passing through the Canal Zone Biological Area, Barro Colorado Island, Canal Zone, from late February to mid-May 1961. Diel variation was reduced, but certainly was not eliminated, in that all were captured in the forenoon.

Freshly caught birds were weighed to the nearest 0.1 gram immediately, to obtain the wet weight, and the visible fat class and molt condition noted. Fat was recorded as a modified McCabe index (McCabe, 1943) that allowed ordering at 14 levels which were later pooled into four classes (Table 1). Molt

¹ Based on part of a doctoral thesis in the Department of Zoology, University of Illinois, Urbana, Illinois.

TABLE 1 Visible Fat Class Description

Assigned quantitative value	Description						
1	From a lean condition with no fat in the furcular depression (interclavicular fossa) to the condition in which the furcular area is well lined with fat and the first definite accumulation of abdominal fat is apparent						
2	Fat beginning to fill the furcular depression, and a sheet of fat almost covering the abdomen						
3	Furcular depression full of fat, and abdomen completely covered with a layer of fat						
4	Furcular area and abdomen bulging with fat						

was determined as light (less than 10 body feathers growing in), medium (10–25 body feathers and/or 2–4 flight feathers growing in), or heavy (more than 25 body feathers and/or 2–4 flight feathers growing in). Captives were provided with food and water ad lib.

Data on thermal-stressed birds were obtained upon their death at high and low temperatures in thermostatically controlled temperature cabinets. After the completion of the postnuptial molt, Dickcissels were exposed to increasingly higher temperatures at 12 hours photoperiod, that of their tropical wintering grounds, and to increasingly colder temperatures at 10 hours photoperiod, that of the coldest month at temperate latitudes. Additional posnuptial captives were subjected to the cold stress of the Illinois winter under outdoor conditions. Summer birds were placed under thermal stress at both high and low temperatures at 15 hours photoperiod, that of the longest day at the latitude of central Illinois. Since with all cabinet birds the temperature was not changed until the birds maintained a constant weight in order that their existence energy requirements could be measured (Zimmerman, 1963), there probably was temperature acclimation prior to finally reaching the lethal limits.

Captives were also held outdoors in the Canal Zone during the winter and spring and were sacrificed for carcass analysis at the peak of vernal fat deposition. The wet weight of both these and the thermal-stressed captives was determined at death.

Most carcasses were frozen until ready for analysis, but birds returned from the Canal Zone and some Illinois specimens were preserved in 95% ethanol. Dry weights, which include the feathers, were obtained after placing the cut-up bird in a vacuum oven at 60–70 C until a constant weight was reached. The

TABLE 2
BODY CONSTITUENTS OF WILD BIRDS—IN GRAMS*

Date	No.	Wet weight	Water	Lipids	Protein	Carbohydrates and ash
Wintering & &						
25 Jan.	2	30.4 ± 0.80	18.070 ± 0.73 (59.4)	4.889 ± 0.47 (16.1)	6.334 ± 0.11 (20.8)	1.108 ± 0.43 (3.6)
15 Feb.	3	29.4 ± 2.44		1.749 ± 0.35 (5.8)	6.389 ± 0.07 (22.0)	1.817 ± 0.19 (6.4)
Wintering ♀♀)		(2212)	, - ,		
25 Jan.	3	23.0 ± 0.91	14.999 ± 0.54 (65.3)	1.126 ± 0.29 (4.9)	5.532 ± 0.02 (24.2)	1.310 ± 0.25 (5.7)
15 Feb.	2	25.9 ± 0.45		3.287 ± 1.21 (12.6)	5.607 ± 0.01 (21.7)	1.358 ± 0.02 (5.3)
Migrating & &						
28 Feb.	2	26.0 ± 0.10	15.691 ± 0.93 (60.4)	3.036 ± 0.82 (11.7)	6.133 ± 0.11 (23.6)	1.140 ± 0.32 (4.4)
8 Mar.	3	28.2 ± 1.48	17.415 ± 0.18 (62.1)	2.920 ± 1.25 (10.0)	6.352 ± 0.09 (22.6)	1.513 ± 0.11 (5.4)
22 Mar.	8	27.7 ± 0.39	17.178 ± 0.27 (62.0)	2.617 ± 0.21 (9.4)	6.354 ± 0.11 (22.9)	
2 Apr.	7	29.0 ± 0.79	16.800 ± 0.29 (58.5)	4.198 ± 0.67 (14.2)	6.135 ± 0.06 (21.2)	1.767 ± 0.08
13 Apr.	3	26.6 ± 1.13	15.679 ± 0.75 (58.9)	3.540 ± 0.26 (13.3)	5.869 ± 0.18 (22.1)	1.545 ± 0.04 (5.8)
Migrating ♀♀)					
28 Feb.	2	23.3 ± 2.45	13.500 ± 1.01 (58.3)	3.245 ± 1.13 (13.6)	5.223 ± 0.22 (22.6)	1.282 ± 0.09 (5.5)
22 Mar.	1	23.8	15.591 (65.5)	1.272 (5.3)	5.625 (23.6)	1.313 (5.5)
2 Apr.	1	27.2	14.507 (53.3)	6.176 (22.7)	5.200 (19.1)	1.317 (4.8)
13 Apr.	3	24.3 ± 1.41	14.643 ± 0.77 (60.4)	2.882 ± 0.54 (11.8)	5.316 ± 0.22 (22.0)	
Breeding & &						
13 June	3	29.3 ± 0.18	19.660 ± 0.28 (67.2)	9.995 ± 0.47 (3.4)	7.142 ± 0.08 (24.4)	1.470 ± 0.08 (5.0)
10 July	4	28.1 ± 0.20	18.766 ± 0.20 (66.8)	0.953 ± 0.07 (3.4)	6.757 ± 0.11 (24.1)	
19 July	4	27.9 ± 0.72	18.759 ± 0.54 (67.2)		6.885 ± 0.20 (24.7)	
27 July	5	28.4 ± 0.61	19.441 ± 0.47 (68.3)	1.030 ± 0.06 (3.6)	6.393 ± 0.13 (22.5)	
8 Aug.	6	29.0 ± 0.30	19.682 ± 0.20 (67.9)	1.144 ± 0.10 (4.0)	6.639 ± 0.18 (22.9)	

^{*} Figures in parentheses are the per cent of wet weight.

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TABLE	2	(Con	tınu	ed)

Date	No.	Wet weight	Water	Lipids	Protein	Carbohydrates and ash
Breeding 9 9						
13 June	3	25.4 ± 1.20	17.175 ± 0.87 (67.7)	1.116 ± 0.16 (4.4)	5.835 ± 0.08 (23.1)	1.241 ± 0.08 (4.9)
10 July	1	24.6	10.903 (68.7)	0.790 (3.2)	5.536 (22.5)	1.371 (5.6)
19 July	1	25.1	16.723 (66.6)	1.324 (5.3)	5.524 (22.0)	1.529 (6.1)
27 July	3	24.9 ± 0.53	16.499 ± 0.29 (66.3)	1.179 ± 0.12 (4.8)	5.588 ± 0.05 (22.6)	1.806 ± 0.58 (7.2)
8 Aug.	1	25.9	17.930 (69.2)	0.757 (2.9)	5.971 (23.1)	1.242 (4.8)

amount of water in the carcass was determined by subtracting the dry weight from the wet weight of the bird at death. Fat determinations are on the basis of ether extractable lipids obtained with a Soxhlet apparatus (see Odum, 1960). There was no difference in the amounts of extractable lipids between frozen birds and those previously treated with alcohol. (Compare lipid amounts of frozen June and early July wild birds with alcohol-preserved wild birds from late July and August, Table 2.) Protein values are based on total organic nitrogen determined by the Kjeldahl method (see Fischer, 1961:229–231).

Procedures for the statistical treatment of data were taken from Dixon and Massey (1957) and Jacob and Seif (mimeo). A probability level of 0.05 was required for significance. The indicated variation associated with the means is the standard error.

CARCASS ANALYSIS OF WILD BIRDS

The body composition of 71 Dickcissels (50 males and 21 females) from both the summer and winter ranges is presented in Table 2 and Figs. 1 and 2.

The greater wet weight of males is significantly different from that of females. This is due to a significant difference in the amounts of protein and water between the sexes. There is no sex difference in the weights of the remainder of carbohydrates and ash or in the weights of the lipids.

The wet weight of neither males nor females showed any significant changes throughout the period of collection. There are positive correlations between wet weight and lipids, water, and protein which are significant in all cases except between wet weight and lipids in females. The weight increase obtained in captives during the vernal migratory period in the Canal Zone was

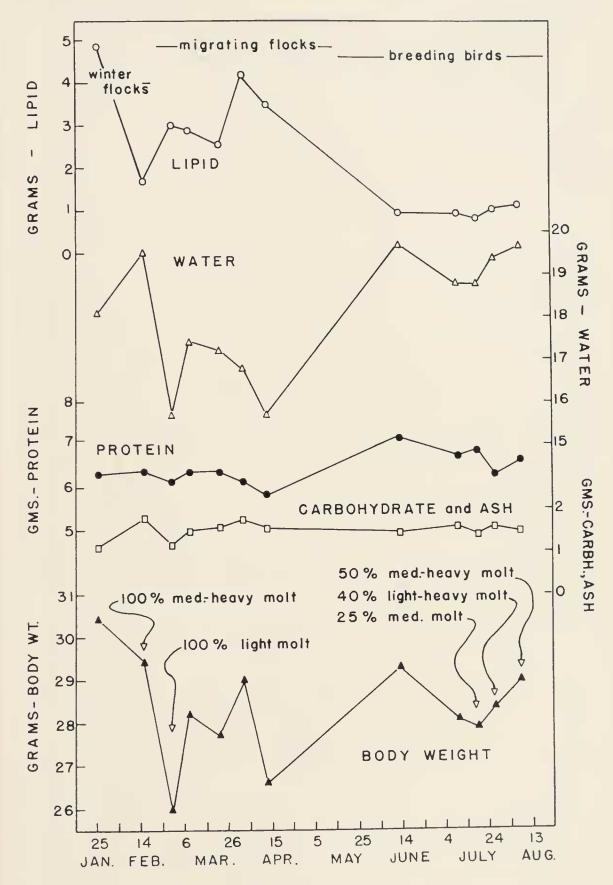


Fig. 1. Carcass components of wild males from January to August. See text for explanation of molt.

TABLE 3

CARCASS ANALYSIS OF HIGH DEPOT FAT, SPRING DICKCISSELS—IN GRAMS*

	Males	Females
Number	7	5
Wet weight	38.4 ± 0.94	32.7 ± 1.01
Water	$19.186 \pm 0.41 $ (50.0)	15.577 ± 0.45 (47.7)
Lipids	$10.876 \pm 0.79 \tag{28.1}$	10.464 ± 0.80 (31.9)
Protein	6.120 ± 0.08 (16.4)	5.000 ± 0.07 (15.3)
Carbohydrates and ash	2.399 ± 0.28 (6.5)	1.699 ± 0.07 (5.2)

^{*} Figures in parentheses are the per cent of wet weight.

not demonstrable in wild-caught birds during the same period. These migrants were netted in the morning following a night of presumed movement, which could have depleted their fat stores, reducing their weight. Helms (1959) has illustrated such an effect in other fringillids. The wet weight in both sexes was most constant during the summer months.

The wintering lipid level of nonmolting birds was high, while the prenuptial molt was correlated with a significant drop in fat. A similar decrease in body lipids associated with this molt has been reported in the White-throated Sparrow (Zonotrichia albicollis) (Odum and Perkinson. 1951) and the White-crowned Sparrow (Z. leucophrys gambelii) (King and Farner, 1959).

During the spring migration the lipid level remained about that of wintering birds except for the high early April value, which in females is significantly different from those at any other time sampled and in males is significantly different from all others except nonmolting winter birds and other migrants. Lipid values of captives killed at maximum spring fat deposition (Table 3) were 2.6 and 1.7 times greater than the early April values in wild males and females, respectively. The effect of early morning capture on fat content has been mentioned above. The lack of significant fat increase during the early migratory period in the Canal Zone, as well as the lower level of the April amounts when compared to obese captives killed a month later, may also be attributed to the possibility that maximum deposition does not occur until later in their migratory journey. A wintering population of the Slate-colored Junco (Junco hyemalis) studied by Johnston (1962) departed without fat reserves, while captives from this population did subsequently undergo

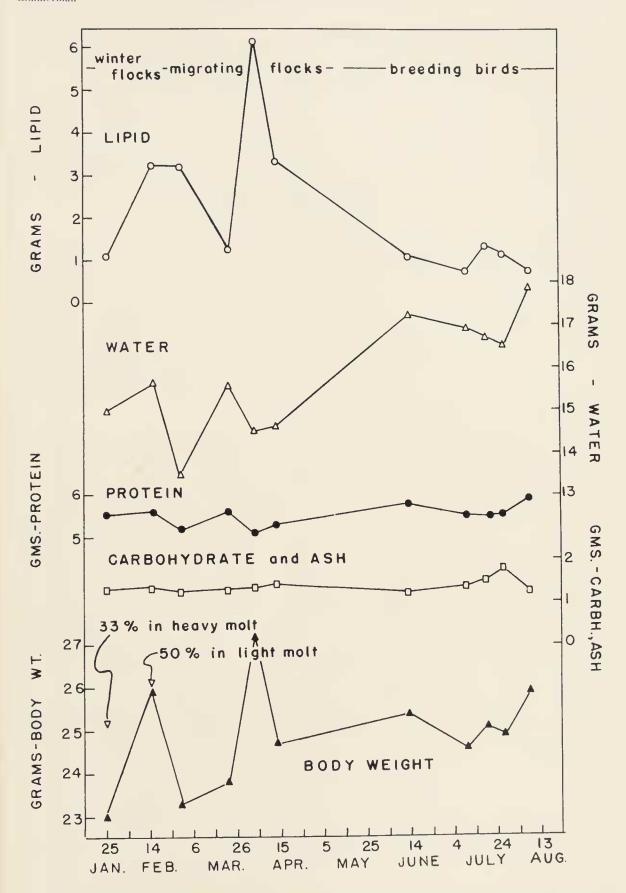


Fig. 2. Carcass components of wild females from January to August. See text for explanation of molt.

vernal fat deposition. Recent data presented by Caldwell, Odum, and Marshall (1963) illustrate a similar situation occurring in wild birds during fall migration.

Although carcass data were not available, the visible fat of birds captured upon arrival in Illinois during late April and early May indicated a lack of appreciable fat stores (Zimmerman, 1963). The lipid content of birds on the breeding grounds remained constant and low, and, being already minimal, was not reduced by the occurrence of the postnuptial molt. No wild birds were obtained during autumnal fat deposition.

The amount of protein remained relatively stable. In females there are no significant differences throughout the period of collection. In males summer values were high; the amounts for 13 June, 19 July, and 10 July are significantly different from any during either winter or spring but similar, for the most part, to the 27 July and 8 August values. The higher protein level in breeding males probably reflects the anabolic action of androgens in protein metabolism (Turner, 1960:343–345), an effect suggested for the high carcass protein in the Canada Goose (*Branta canadensis*) during the summer (Hanson, 1962; Williams, 1964).

There are no significant differences from January to August in the water content of females, but values were highest in breeding birds and lowest in migrants. Males had similar trends, although generally winter and summer birds were similar. Like the females, the amount of water was lowest during migration. The values for 28 February, 2 April, and 13 April are significantly different from all others except the other migrant samples and that of 25 January. Since these migrating birds were obtained in the morning, these low values reflect the dehydrating effect of a night of active migration, an average decrease of as much as 4% of the wet weight when compared to wintering birds. This contention is supported in that the obese May-killed captives (Table 3) had water amounts similar to leaner, nonmigrating wild birds (Table 2).

The remainder, mostly ash and some carbohydrate, was constant from January to August. There are no significant changes in the females. There are significant differences between some values at the extremes of the range in males, but no relationship exists with the time of year.

FAT CLASS AND BODY CONSTITUENTS OF WILD BIRDS

With data grouped according to visible fat class (Fig. 3), there is no significant correlation in either sex between wet weight and water or between wet weight and the fat-free dry weight. While the coefficients of correlation between wet weight and the weight of the lipids are also not significantly different from zero with just four fat classes (males: r = 0.859, females: r = 0.859).

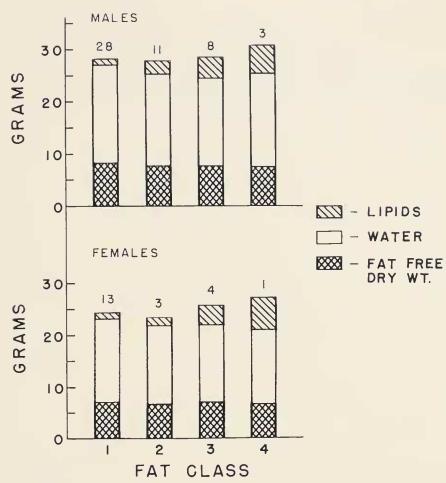


Fig. 3. Lipids, water, and fat-free dry weight of wild males and females according to visual fat classes. The number at the top of each histogram is the sample size for that fat class.

0.948), the magnitude of these coefficients does suggest a strong positive relationship between the average wet weight and the amount of lipids in these fat classes.

Birds were initially placed in one of 14 visible fat categories, but upon analysis of their lipid content it was realized that these original fat classes were not truly indicative of the fat reserves available to the birds. This was particularly evident in the first 8 of these 14 classes in which lipid quantity, while generally increasing with each category, still did not increase by a statistically significant amount between class 1 and class 7. Since there is no difference between the sexes in the weights of their lipids, data from both sexes were pooled for each of the four fat classes described in Table 1, and the lipid quantities of these fat classes are significantly different from each other.

TERMINAL CARCASS ANALYSIS AFTER THERMAL STRESS

For all Dickcissels under constant photoperiod conditions, over one-half of the birds could sustain an existence level energy balance as indicated by

TABLE 4
TERMINAL BODY CONSTITUENTS—IN GRAMS*

	Under Hea	nt Stress		
	12 hr (postnuptial)	15 hr (summer)		
6 8				
Wet weight	21.4 ± 4.40	18.8 ± 0.79		
Water	10.619 ± 0.87	11.332 ± 0.49		
	(50.9)	(60.2)		
Lipids	3.774 ± 3.10	0.815 ± 0.26		
	(15.3)	(4.0)		
Protein	5.235 ± 0.17	5.419 ± 0.12		
	(25.4)	(28.9)		
Carbohydrates and ash	1.772 ± 0.26	1.273 ± 0.01		
	(8.4)	(6.8)		
Number	2	8		
9 9				
Wet weight	16.2 ± 0.49			
Water	9.259 ± 0.36			
	(57.3)			
Lipids	1.129 ± 0.51			
	(6.8)			
Protein	4.637 ± 0.27			
	(28.6)			
Carbohydrates and ash	1.175 ± 0.06			
	(7.2)			
Number	3			

^{*} Figures in parentheses are the per cent of wet weight.

their maintenance of a constant weight over a 3-day period at any given temperature up to (heat stress) or down to (cold stress) the lethal temperature. The lethal temperature, then, is the temperature at which at least 50% of the birds under the respective conditions were in constant negative energy balance leading eventually to death within 24 hours for most but only after several days for a few.

The upper lethal limit of temperature tolerance in birds after the fall molt at 12 hours photoperiod and in summer birds at 15 hours was 44 C. The lower lethal limit for birds after the completion of the postnuptial molt at 10 hours photoperiod was -1 C, and for summer birds at 15 hours was -2 C. Birds exposed to the outdoor conditions of the Illinois winter experienced 50% mortality at a mean daily temperature of -3 C. The carcass analyses of these birds are compiled in Table 4, and the statistical relationships are presented in Table 5. The differences between body components were related not to

Table 4 (Continued)

	Under Cold Stress						
	15 hr (summer)	10 hr (postnuptial)	Outdoors (postnuptial				
8 8							
Wet weight	22.4 ± 0.20	22.8 ± 0.65	24.2 ± 0.28				
Water	14.819 ± 0.23	14.883 ± 0.53	16.008 ± 0.24				
	(66.0)	(65.3)	(66.2)				
Lipids	0.371 ± 0.02	0.293 ± 0.02	0.367 ± 0.05				
	(1.7)	(1.3)	(1.5)				
Protein	5.631 ± 0.10	5.949 ± 0.19	6.069 ± 0.06				
	(25.1)	(26.2)	(25.1)				
Carbohydrates and ash	1.617 ± 0.04	1.659 ± 0.10	1.739 ± 0.03				
	(7.2)	(7.3)	(7.2)				
Number	8	6	11				
9 9							
Wet weight		19.4 ± 0.17	20.8 ± 0.48				
Water		12.922 ± 0.15	13.834 ± 0.42				
		(66.7)	(66.4)				
Lipids		0.228 ± 0.02	0.310 ± 0.05				
		(1.2)	(1.5)				
Protein		4.853 ± 0.10	5.129 ± 0.10				
		(25.1)	(24.7)				
Carbohydrates and ash		1.372 ± 0.08	1.547 ± 0.07				
		(7.1)	(7.5)				
Number		4	5				

photoperiod, sex. or season, but as might be expected, to the nature of the thermal stress.

The terminal wet weight of heat-stressed birds was lower due to a marked dehydration as well as generally lower protein and carbohydrate and ash levels. Lipids were highest in this group. Death at the upper limit of temperature tolerance probably develops from a variety of effects ramifying from the disruption of homeostasis by increasing hyperthermia. Heat death is not due to the exhaustion of energy stores depleted by a high metabolic rate, since terminal fat reserves were high. The reduction in the free water content of these birds, resulting from the utilization of most available water for evaporative heat loss from the respiratory tract, may be the proximal factor responsible for death. The increased water requirement at high temperatures has been illustrated in birds by several authors (Bartholomew and Cade, 1956; Bartholomew and Dawson, 1954; Kendeigh, 1944), and the im-

TABLE 5

RANK AND DIFFERENCES OF THE VARIOUS CARCASS CONSTITUENTS ACCORDING TO ENVIRONMENTAL CONDITION*

		Heat	Heat stress		Cold stress		
		12 hr	15 hr	15 hr	10 hr	Outdoors	
Wet weight	8 8	$2^{1\cdot 2}$	11	3^2	4^{2}	5^2	
	9 9	1^{1}			2^2	3°	
Lipids	88	5^{2}	4^1	3^{1}	11	2^{1}	
	9 9	3^{2}			11	2^{1}	
Water	3 3	1^1	2^1	3^{2}	4^2	5^{2}	
	9 9	1^{1}			2^2	3^{2}	
Protein	88	1^1	2^1	$3^{1, 2}$	$4^{2.3}$	5^{3}	
	9 9	1^1			2^1	3^{1}	
Carbohydrate and ash	88	5^{2}	l^1	2^2	3^{2}	4^{2}	
	9 9	1^1			2^{1+2}	3^{2}	
Season		Winter	Summer	Summer	Winter	Winter	

^{*}The rank of the means for each comparison (across) are numbered from lowest to highest. Means (see Table 4) which are *not* significantly different have the same superscript associated with their rank numbers.

portance of water in thermoregulation (Dawson, 1954) and its limits as a means of heat dissipation (Dawson, 1958; Kendeigh, op. cit.) have been described.

In cold-stressed birds the terminal wet weight was greater than that of birds dying at high ambient temperatures, even though lipid levels were almost nil, due to the greater amounts of the other fractions. Among these cold-stressed birds, those under outdoor conditions had the highest, although not always significantly so, levels of all components except the negligible lipids. Most of these birds died at lower environmental temperatures than those at cold, constant temperatures. Both these differences in the outdoor individuals are probably related to the fluctuating temperature which allows short, daily reprieves from near lethal conditions, and death results from the effects of the relatively short, but intense, nightly low. Birds at constant temperatures, on the other hand, suffer continuing attrition under unvarying cold stress and die "earlier" but more exhausted.

The weights of body constituents in wild summer birds were compared with summer birds under heat and cold stress at 15 hours, and the weights of components in wild winter birds were compared with postnuptial birds under heat stress at 12 hours and cold stress at 10 hours and outdoors. Thermal stress, no matter at which extreme, reduced the weights of protein and water when compared to wild birds at the same season. The weights of lipids are similar in heat-stressed captives and wild birds in both summer and winter.

TABLE 6
ESTIMATED CARBOHYDRATE LEVELS*

		Wild -	Cold stress		Heat stress		High depot	
			15 hr	10 hr	Ontdoors	15 hr	12 hr	fat captives
Remainder, % dry wt	8 8 9 9	15.4 15.6	21.4	21.1 21.2	21.3 22.2	17.0	17.5 17.2	13.0 9.9†
Carbohydrates, % dry wt	\$ \$ \$ \$	3.4 3.6	9.4	9.1 9.2	9.3 10.2	5.0	5.5 5.2	1.0 0.0
Estimated dry wt of carbohydrates	δ δ	0.342 0.321	0.716	0.719 0.594		0.375	0.593 0.361	0.193 0.0
Number	8 8 9 9	50 21	8	6 4	11 5	8	2 3	5 5

* Based on Turček's (1960) estimate of ash as 12% of dry weight with s = 1.5%.

† This value is within 2s of Turček's average and assumed to include no carbohydrate portion.

but the cold-stressed individuals are lower than all three. The weight loss of mice exposed to lethal cold temperatures was similarly due mostly to utilization of fat reserves plus some reduction in protein and water (Hart and Heroux, 1956). In most cases the weights of the remainder of ash and carbohydrate are similar in wild and thermal stressed birds.

ESTIMATION OF CARBOHYDRATE AMOUNTS

After the removal of water, the extraction of lipids, and the determination of protein, there is a remainder composed of ash and carbohydrates. Turček (1960) gives the ash value of the passerines analyzed as 12% of the dry weight. Using this value, an estimation of the amounts of carbohydrates was made (Table 6). These approximations are consistent with the conditions at death, using the quantity in wild birds as a point of reference. Even at death, cold stress values are high, indicating a high level of gluconeogenesis in connection with thermoregulation, as previously evidenced in the reduced lipid levels, while the content in heat-stressed birds is lower and more like that of the wild population. Birds at temperatures above thermal neutrality are not concerned with calorigenesis. The very low levels in birds during the peak of fat deposition are corroborated by the findings of Farner et al. (1961) which show a reduction in the glycogen content of liver and pectoral muscle at this time.

SUMMARY

The greater weight of males is significantly different from that of the females due to the higher levels of protein and water. Amounts of lipids and the carbohydrate-ash remainder show no sex differences.

A spring migratory weight peak could not be illustrated in wild birds; and although the fat content of migratory birds in early April was high, it was much lower than the quantity extracted from obese premigratory captives. Early morning capture and the later occurrence of maximum fat deposition are suggested as factors responsible for these lower lipid levels. Dehydration by a night of migration is apparent in the free water content of migrants.

Winter lipid levels in wild birds were reduced by the prenuptial molt. Amounts of lipids in both sexes on the breeding grounds were constant and, being already minimal, were not affected by the postnuptial molt.

Significantly higher amounts of proteins were found in males during the breeding season.

There is a significant difference in the amount of lipids between each of the four visible fat classes that were used in this study.

Birds dying under cold stress had negligible lipids, while carcasses of heat-stressed birds were high in lipids, but low in water. Under both extremes of thermal stress, the weights of protein and water were less than that of wild birds at the same season.

Estimates of the amounts of carbohydrates revealed similar levels in heat-stressed birds and wild birds, high levels in birds dying under cold stress, and very low amounts in birds at the peak of vernal fat deposition.

ACKNOWLEDGMENTS

Great appreciation is due Dr. S. C. Kendeigh, who directed the study. I would also like to thank J. B. Olson and J. E. Williams for aid in collecting specimens, and S. A. Olson and J. Zar for the biochemical analyses. Thanks are also due to Dr. M. Moynihan and his staff at the Canal Zone Biological Area for making it possible to complete the tropical phase of this research. This project was financed by grant G 14261 from the National Science Foundation.

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